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ONTOGENETIC SHAPE CHANGES IN THE SKULL OF *SCAPHONYX FISCHERI* WOODWARD, 1907 (ARCHOSAUROMORPHA, RHYNCHOSAURIA, RHYNCHOSAURIDAE) USING THIN-PLATE SPLINES ANALYSIS[1]

(With 2 figures)

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ABSTRACT: Ontogenetic shape changes in skull shape of the rhynchosaur *Scaphonyx fischeri* Woodward, 1907 from the Santa Maria Formation (Triassic of Rio Grande do Sul, Brazil) were studied using the geometric method of thin-plate splines. The method was applied to a set of 15 anatomical landmarks taken from scanned drawings of the dorsal face of four *Scaphonyx* skulls representing different growth stages. The analysis indicated that most of the ontogenetic allometry occurs along the transversal axis of the skull, and can be described by an elongation of the facial and temporal surfaces of the skull and an increase of the interorbital region. These results are consistent with previous analyses of these skulls performed with the original method of deformed coordinates of D'Arcy Thompson.

Key words: geometric morphometrics, thin-plate splines, transformation grids, ontogeny, rhynchosaurs.

RESUMO: Análise da modificação ontogenética da forma do crânio de *Scaphonyx fischeri* Woodward, 1907 pelo método de deformações parciais.

As mudanças ontogenéticas na forma do crânio do rincossauro *Scaphonyx fischeri* Woodward, 1907 da Formação Santa Maria (Triássico do Rio Grande do Sul, Brasil) foram estudadas usando o método geométrico de análise de deformações. O método foi aplicado a um conjunto de 15 marcos anatômicos digitalizados a partir das ilustrações da face dorsal de quatro crânios de *Scaphonyx*, representando diferentes estágios de crescimento. A análise indicou que a maior parte da alometria ontogenética ocorre ao longo do eixo transversal do crânio, podendo ser descrita por um alongamento das superfícies facial e temporal do crânio e um aumento da região interorbital. Esses resultados são consistentes com prévias análises realizadas pelo método original das coordenadas deformadas de Thompson.

Palavras-chave: morfometria geométrica, análise de deformações, coordenadas deformadas, ontogenia, rincossauros.

INTRODUCTION

Morphometrics, the study of shape and shape changes in organisms, has recently undergone a revolution with the development of the new concepts and techniques of the so-called "geometric morphometrics" (ROHLF & MARCUS, 1993). Geometric morphometrics distinguishes and analyzes differences in size and shape based on Cartesian coordinates of discrete landmarks, the location of which is assumed to be homologous and can be unambiguously determined in all the organisms under study.

Thin-plate splines analysis (BOOKSTEIN, 1989, 1991) is one of the most important geometric morphometrics tools. The graphical output of this technique closely resembles the method of "transformation grids" for depicting shape changes between two organisms as deformations, introduced by THOMPSON (1917). However, thin-plate splines analysis is based on a well-founded mathematical approach that allows the exact mapping of the transformation of the landmark configuration of one organism into that of another, and leads to a rigorous quantitative description of the spatial organization of shape changes. On the other hand, Thompson's deformed coordinates are not based on any analytical method and do not require the explicit specification of landmarks used to depict the transformations of shape. As the transformation grids of the method of deformed coordinates are often sketched subjectively, they are not amenable to comparisons among different studies of the same group of organisms.

The results of principal warps analysis using thin-

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plate splines interpolation functions are frequently compared in the literature to Thompson's method. However, no empirical tests have been performed to assess the differences and similarities between the results of these two approaches, beyond mere subjective evaluations of overall resemblance in graphic representation.

Rhynchosaurs constitute an abundant group of herbivorous diapsid reptiles with a widespread geographical distribution, but temporally restricted to Triassic times. The systematics of this group is currently under discussion, which begun with the works of SCHULTZ (1991) and SCHULTZ & BARBERENA (1991). LANGER & SCHULTZ (2000) provide a recent overview, including a phylogenetic study of the Rhynchosauridae. BARBERENA (1971) employed Thompson's transformation grids to study ontogenetic changes in cranial shape in four specimens of *Scaphonyx fischeri* Woodward from the Vila Kennedy outcrop, within the red sandstones of the Santa Maria Formation (Middle Triassic of Rio Grande do Sul, Brazil). He concluded that the differences in shape observed among these specimens were more probably due to growth processes, while not excluding the possibility that such modifications were the result of differences in diet, sexual dimorphism, or intraspecific variation. BENTON & KIRKPATRICK (1989) also applied transformation grids to depict shape changes in ontogenetic series of *S. fischeri*, using the drawings from BARBERENA (1971) plus a juvenile specimen described by them. Their findings supported the conclusions of BARBERENA (*op. cit.*) on the growth patterns of *S. fischeri* and also suggested the occurrence of an heterochronic shift in the ontogeny of this species.

The aim of the present study was to compare the results of a thin-plate splines analysis with those obtained by BARBERENA (1971) using Thompson's original method of transformation grids, in order to empirically test for differences and similarities between the results of these two approaches. It should be emphasized that our primary goal is to compare these two methodologies and not to perform a detailed morphometric study of growth patterns in *Scaphonyx fischeri*.

MATERIAL AND METHODS

Line drawings on page 405 of BARBERENA (1971) were digitized with a desk scanner attached to an IBM-PC microcomputer. Pictures were acquired, processed, and saved in JPEG format at high resolution (600 dpi), using the Adobe Photoshop image-processing program. Coordinates for 15 landmarks were taken from the digitized images by means of the TpsDig program written by F.J. Rohlf, version 1.18. Landmarks were collected on the right half of the skull only, in order to avoid the disturbing effects of lateral asymmetry (BOOKSTEIN, 1996).

The method of thin-plate splines (BOOKSTEIN, 1989, 1991) was used to model ontogenetic shape changes among the landmarks as a deformation. The analysis by splines consists in fitting an interpolating function to the x, y landmark coordinates for each specimen so that all homologous landmarks coincide. For the computation of this function, a reference configuration is kept fixed, and another or others are superimposed so that each landmark is forced to coincide with its homologous in the reference. Differences in shape are reported as the energy (the "bending energy"), associated to the deformation of a theoretically idealized thin metal plate. The eigenvectors of the bending energy matrix are called "principal warps", and are relative only to the reference. The eigenvalues associated to each principal warp are an inverse measure of the spatial scale of shape change, so that large eigenvalues correspond to small-scale deformations and small eigenvalues correspond to large-scale deformations. The projection of the specimens onto the principal warps yields the "partial warps", that describe their deviations from the reference configuration.

In this study, the reference configuration was determined in two ways: 1) using the first specimen (Specimen A) as the reference, as done by BARBERENA (1971); 2) as the consensus (average) configuration of the four specimens from a generalized least-squares orthogonal Procrustes analysis (ROHLF & SLICE, 1990). The purpose of the reference is to define the linear tangent space that is used to approximate the non-linear true shape space (ROHLF, 1996).

The bending energy required to deform the configuration of landmarks in the reference into those of each specimen was computed, along with a symmetric matrix of bending energies between all pairs of specimens. All values were computed using the bending energy metric (using the inverse of the bending energy matrix) based on the reference specimen. In addition, the Procrustes distance between each specimen and the reference was also computed both as a linear distance and as a geodesic distance (angles in radians). All computations were performed using F.J.Rohlf's TpsSplin program, version 1.15.

RESULTS AND DISCUSSION

Ontogenetic shape changes depicted as thin-plate splines Cartesian deformations are shown in figures 1 and 2. The specimens A to B and B to D seem to truly constitute an ontogenetic series, characterized by a lateral expansion of the temporal region. On the other hand, specimen C shows a pronounced bi-directional expansion of the upper temporal region. These results closely resemble those of BARBERENA (1971), but do not support his suggestion that both specimens, C and

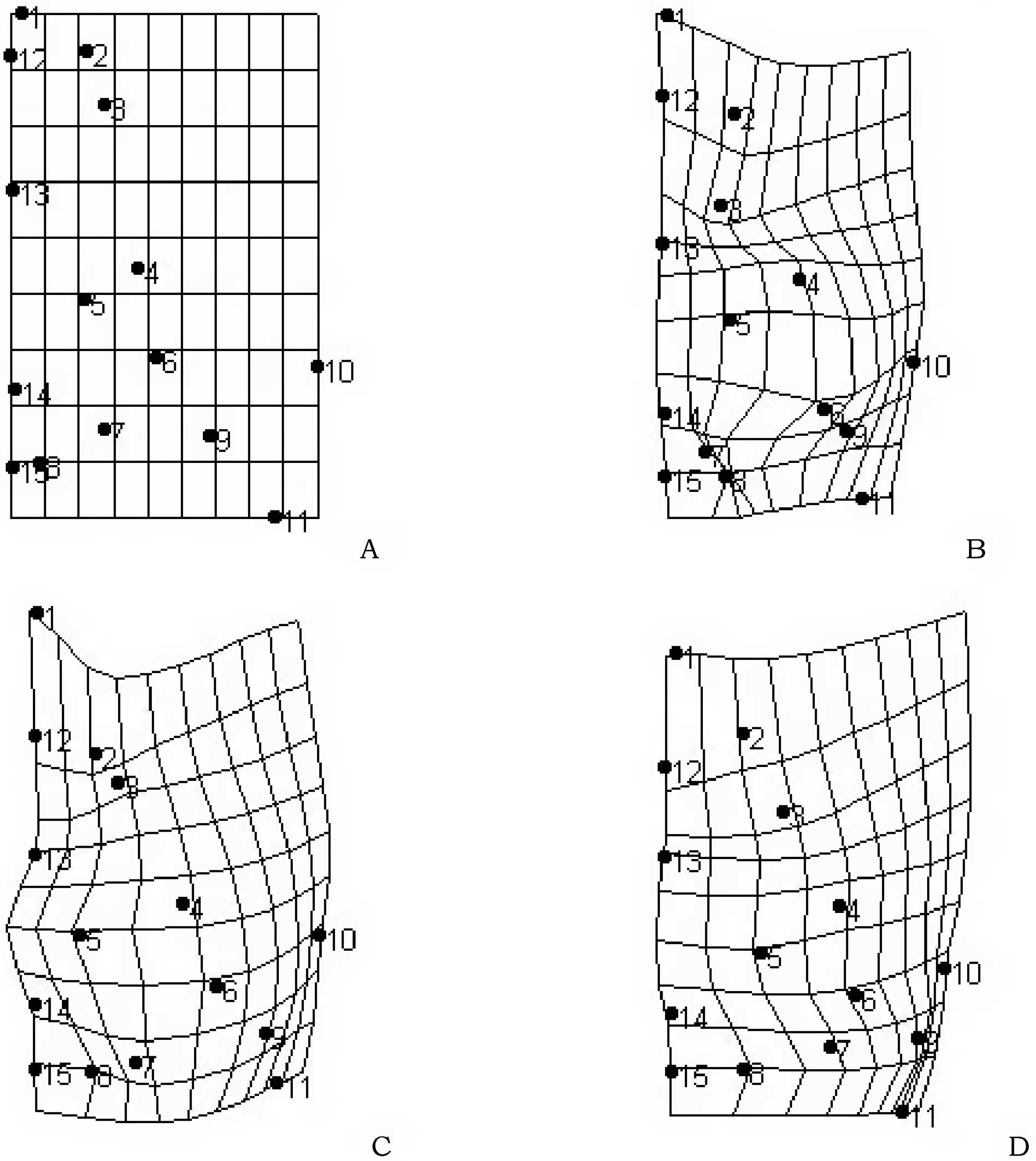

Fig.1- Cartesian grids for the specimens of *Scaphonyx fischeri* Woodward, 1907 as deformations using specimen A as the reference configuration.

D, would belong to different taxa. According to our thin-plate splines analysis, only specimen C would belong to another taxon, with the other specimens possibly constituting the members of a true ontogenetic series.

Bending energy, Procrustes distances, and angles (in radians) between each specimen and the specimen A considered as the reference are shown in table 1. These data indicate that the bending energy needed to deform specimen C into the reference was considerably higher than that required by the other specimens.

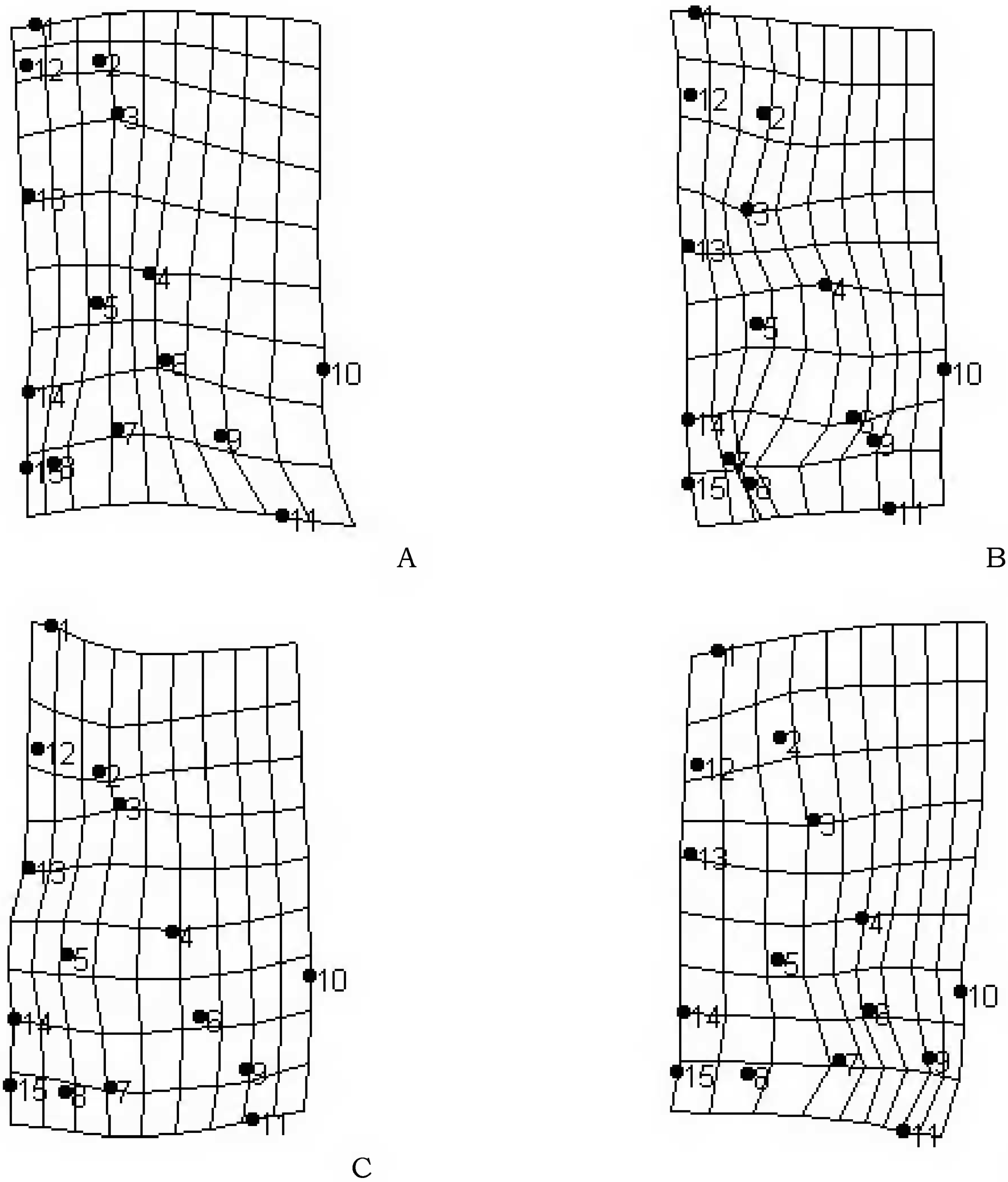

Fig.2- Cartesian grids for the specimens of *Scaphonyx fischeri* Woodward, 1907 as deformations using the average configuration of the four specimens as the reference configuration.

TABLE 1

Bending energy, Procrustes distances, and angles (in radians) between each specimen and the specimen A used as the reference

Specimen	Energy	d	Angle
A	0.25255	0.12753	0.12788
B	0.60569	0.11939	0.11968
C	0.19202	0.09446	0.09461
D	0.37256	0.12096	0.12126

Table 2 shows the same information using the average configuration as reference (Fig.2). In this case, there seems to be an influence of the discrepant shape changes presented by specimen C on the results, with this specimen being closer to the average configuration than the other ones. This interpretation is supported by the figures of all three numerical parameters used for the comparisons.

SCHULTZ (1991) studied the specimens analysed by BARBERENA (1971) and concluded that two of the skulls (specimens A and D) present deformations resulting from diagenetic processes common in the Santa Maria Formation (HOLZ & SCHULTZ, 1998), that are prone to disturb any morphological analysis of these specimens. Specimen A poses special problems, since its fossilization involved a strong dorso-ventral compression and the drawing by BARBERENA (1971) did not take this deformation into account. Specimen D, on the other hand, is not deformed by compression but presents alterations of volume due to diagenetic processes. While such considerations should be kept in mind in interpreting the results of the present study, we do not believe that they would modify the overall results of our metodological comparison in any significant way. Indeed, the very fact that it was specimen C (and not the problematical A or D) which appeared as the most deformed in our analyses seems to support this contention.

TABLE 2

Bending energy, Procrustes distances, and angles (radians) between each specimen and reference, taken as the average landmark configuration of the four specimens

Specimen	Energy	d	Angle
A	0.00000	0.00000	0.00000
B	3.64626	0.19246	0.19367
C	4.69094	0.19518	0.19644
D	3.93195	0.20672	0.20822

As stated before, the primary purpose of this study was to compare the analytical technique of thin-plate splines applied to 2D configurations of landmarks to Thompson's Cartesian grid deformations, as methods of describing shape changes in biological forms. Our results have partially supported the analysis of BARBERENA (1971), with a few important differences not detected by that author, stressing the accuracy of the geometric morphometric procedure. Other procedures should be used to study variation within a sample (especially when there are more than just a few specimens), to compare groups of configurations, or to relate shape variation to an independent variable (ROHLF, 1998). We expect that this type of analysis also bring some light on the discussions currently under way concerning the taxonomic status of the genus *Scaphonyx* in South America.

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